



The economic impacts of ocean acidification on shellfish fisheries and aquaculture in the United Kingdom

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ABSTRACT

Ocean acidification may pose a major threat to commercial fisheries, especially those for calcifying shellfish species. This study was undertaken to estimate the potential economic costs resulting from ocean acidification on UK wild capture and aquaculture shellfish production. Applying the net present value (NPV) and partial equilibrium (PE) models, we estimate both direct and economy-wide economic losses of shellfish production by 2100. Estimates using the NPV method show that the direct potential losses due to reduced shellfish production range from 14% to 28% of fishery NPV. This equates to annual economic losses of between £3 and £6 billion of the UK's GDP in 2013, for medium and high emission scenarios. Results using the PE model showed the total loss to the UK economy from shellfish production and consumption ranging from £23–£88 million. The results from both the direct valuation and predicted estimate for the economic losses on shellfish harvest indicate that there are regional variations due to different patterns of shellfish wild-capture and aquaculture, and the exploitation of species with differing sensitivities to ocean acidification. These results suggest that the potential economic losses vary depending on the chosen valuation method. This analysis is also partial as it did not include a wider group of species in early-life-stages or predator-prey effects. Nevertheless, findings show that the economic losses to the UK and its devolved administrations due to ocean acidification could be substantial. We conclude that addressing ocean acidification with the aim of preserving commercially valuable shellfish resources will require regional, national or international solutions using a combined approach to reduce atmospheric CO₂ emissions and shift in focus to exploit species that are less vulnerable to ocean acidification.

1. Introduction

Ocean acidification occurs as seawater absorbs atmospheric levels of carbon dioxide (CO₂). Atmospheric CO₂ has increased over recent years and is projected to increase further by the end of the century as fossil fuel reserves continue to be exploited (IPCC, 2001; Caldeira and Wickett, 2003; Blackford and Gilbert, 2007; Doney et al., 2009). Observational studies suggest that the absorption of CO₂ has already decreased pH levels in the global ocean by 0.1 pH units since 1750 (Orr et al., 2005) and that the present rate of change is faster than at any time during the last 55 million years (Pearson and Palmer, 2000). In the UK/European shelf seas, results from observations and modelling studies have shown that CO₂ levels in the near-surface seawater can currently vary between 200–450 ppm, contributing to a pH change of as much as 0.1 units. Recent studies have demonstrated an overall decreasing trend in pH of -0.0035 ± 0.0014 per year, indicating rapid

acidification for the surface (Williamson et al., 2017). These systems will be subject to variability. In most cases the main effect will be attributable to temperature changes which are extremely variable over spatial and temporal scales in shallow shelf seas. These changes will considerably modify i) CO₂ solubility hence pH, ii) biological processes such as photosynthesis and respiration, which contributes to an up-take and CO₂ release, and iii) riverine inputs from anthropogenic sources, that will contribute to enhanced biological production (Williamson et al., 2013; 2017).

The potential direct biological impacts of ocean acidification occur at both the molecular and cellular level (Kroeker et al., 2013; Le Quesne and Pinnegar, 2012), and will act to diminish the ability of calcifying organisms to construct their shells or skeletons, especially affecting species with a low level of biological control over the calcification process. Ocean acidification and decreasing carbonate ion concentration could therefore directly impact organisms including molluscs and

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Table 1
Responses of molluscs and crustaceans based on selected literature review on the biological experiments conducted between 2005–2015. Total published materials on “ocean acidification” count 89,993 through Science Direct database of which publication title, Marine Pollution Bulletin (275), Marine Chemistry (421), and Climate related (274). Studies used to calculate effect sizes for mollusc and crustaceans are highlighted in bold.

Authors *multi-species experimental design	Category Molluscs & Crustaceans	Species	Life-cycle stages/ experimental duration	Effect level biological processes vs pH, CO ₂
Fabry et al. (2008); Lannig et al. (2010); Vengatesen and Ko (2012); Dineshram et al. (2012); Ivanina et al. (2013*); Götz et al. (2014*); Gazeau et al. (2010); Havenhand and Schlegel (2009); Barros et al. (2013); Omer et al. (2013*); Fabry et al. (2008); Duarte et al. (2014); Fitzer et al. (2014); Berge et al. (2006); Gazeau et al. (2010); Bressan et al. (2014)*; Wang et al. (2015); Navarro et al. (2013)	Oyster Oyster + clam*	Crassostrea gigas Crassostrea angulata Crassostrea virginica, Mercenaria mercenaria	2 hours Veliger larvae, 28 days, embryonic development Juvenile	10% decrease in calcification rate, energy, and primary & nucleotide metabolism, cytoskeleton structure. Decreasing calcification with increasing CO ₂ and decreasing pH, salinity, temperature, pH, pH 7.4 in low-salinity larval shell smaller, shell 16%, calcium content 42 in CO ₂ , no response in shell thickness*, sperm motility. 740 ppm; 1036–2008 ppm; 7.55–8.07; 7.9, 7.6, 7.4; 7.76–8.16; ~395, 800, 1500 pCO ₂ : 800–2000 pCO ₂ .
Fabry et al. (2008); Duarte et al. (2014); Fitzer et al. (2014); Berge et al. (2006); Gazeau et al. (2010); Bressan et al. (2014)*; Wang et al. (2015); Navarro et al. (2013)	Mussel Mussel + clam*	P. purpuratus Mytilus edulis Bivalve	Shell dissolve Juvenile Adult & juvenile 44 days, juveniles, 75 days	25% decrease in calcification rate, mortality. Shell diss. No effect by temperature but CO ₂ level. Not aragonite in juvenile shells, 6 month. Shell growth reduced between pH 6.67 and 7.1. 23 days mortality. Different mode between clam and mussel in survival, growth, and shell integrity from OA, temperature, no changes. 7.1/740 ppm; 12–16 °C/390, 700, 1000 ppm; 380, 550, 750, 1000 pCO ₂ ; 6.7–8.1; pH 7.4/3 – 6 months; ~380, ~750, ~1200 pCO ₂ ; 7.67–8.25 Reduced thermal tolerance, mortality reduced in acidified treatments.
Fabry et al. (2008); Clements and Hunt (2014); Range et al. (2011) Klok et al. (2014)	Clam Cockle	M. mercenaria Ceratosma edule	5 days	7.0–7.2, 6.8–7.8 Reductions on shell length, shell weight, cockle flesh over CO ₂ , DEB but difficult to differentiate between assimilation, maintenance and growth 6.7–8.3
Fabry et al. (2008); Sanders et al. (2013)	G. Scallop Scallop + prawn	P. magellanicus P. maximus	77 days	Decrease in fertilization, development DNA and RNA clearance rates, respiration rates, condition index and cellular turn over. < 8.0; 7.82–8.18, temp 15°C
Hendriks et al. (2010)	Mollusc	Bivalve	Larvae Gametes	Calcification & fertility, fertility & growth, primary production, respiration, survival. 0.86 ± 0.093, 1.02 ± 0.015, 0.91 ± 0.031, 0.99
Van Colen et al. (2012)		Macoma balthica	Egg, larvae, embryos	Effects in fertilization, embryogenesis and reduction of larval development. 7.8–8.5
Hendriks et al. (2010)	Crustacean		Larvae	Fertility growth. 0.89 ± 0.081
Fabry et al. (2008); Long et al. (2013); Small et al. (2010); Walther et al. (2009, 2010, 2011); Haye et al. (2011); Hammer et al. (2012); Schiffer et al. (2014) Styf et al. (2013); Hemmroth et al. (2012, 2015)	Crab Nephrop	C. pagurus, N. puber, P. camtschaticus, Necora puber Nephrops norvegicus Hyas araneus	Shell dissolve Juveniles 30 days Eggs, 16 weeks Larvae	Intracellular acid/base disruption, lack of pH regulation, decreased survival, metabolic resistant to low pH. 10000 ppm; 7.98–6.04/0.08–6.04 kPa; pH 7.7; 6.0–8.05; low pH 6.8; 7.4, 6.9, 6.6, 6.3. Embryonic responses % yolk consumption, mean heart rate, oxygen consumption, oxidative stress, larvae for higher metabolic costs, no survival effect by pCO ₂ , THCs 35% reduced. 0.4 units, temp 5–18°C; Tem. 5, 10, 12, 14, 16, 18 & low pH. Decreased survival, growth, egg production. 7.6–7.9; pCO ₂ . 8.2, 7.8, 7.6 pH. 10–18°C, 7.84–8.10 (larvae), 14°C 7.95–7.96 (juvenile)
Kurihara et al. (2008); Donohue et al. (2012); Zheng et al. (2015) Kurihara et al. (2008); Richards et al. (2015*)	Shrimp Prawn, Prawn + scallop*	Palaemon pacificus Palaemon elegans	Egg juvenile, 30, 15 weeks 30 days	Growth slows at 10°C after 5 wks no effect in stage 4. Deformities in larvae and juveniles
Agnalt et al. (2013)	Lobster	Homarus gammarus	Larvae/juvenile, 140 days	Metabolic activity, respiration. Increased pCO ₂ increases a high metabolic rate on the gastropod.
Lardies et al. (2014) Manríquez et al. (2014) Vargas et al. (2014) Vargas et al. (2014) Duarte et al. (2014)	Mollusc Mollusc Mollusc Mollusc Mollusc	C. concholepas juvenile C. concholepas larvae C. concholepas larvae Perumytilus purpuratus Mytilus chilensis	Juvenile/72 hrs Larvae, weeks Larvae, 6 weeks Larvae, 6 weeks Juvenile, 60 days	Changes in survival and hatching success at elevated CO ₂ conditions High pCO ₂ levels influenced the larvae ingestion and clearing rates Negative effect of elevated pCO ₂ on the clearance and ingestion rates Negative effects of the OA were found on growth and net calcification rates of this species over shell deposition, but not by the shell dissolution processes.
Berge et al. (2006) Sanders et al. (2013) Talmage and Gobler (2010)	Mollusc Mollusc Mollusc	Mytilus edulis Pecten Maximus Argopecten irradians	Adult, 44 days Juvenile, 3 months Larvae, 36 days	Results showed induced CO ₂ resulted in a reduction of pH affects the growth of M. edulis negatively Results suggests that abundant food helped to counter balance any effects from changes in water chemistry High CO ₂ concentrations resulted in malformation and erosion of shells. Growth was also affected under high CO ₂ conditions.
Talmage and Gobler (2010)	Mollusc	Mercenaria mercenaria	Larvae, 36 days	High CO ₂ concentrations resulted in malformation and erosion of shells. Growth was also affected under high CO ₂ conditions when compared with pre-industrial rates of pCO ₂ concentrations.
Heinemann et al. (2012)	Mollusc	Mytilus edulis	Adults, 3 months	

(continued on next page)

Table 1 (continued)

Authors *multi-species experimental design	Category Molluscs & Crustaceans	Species	Life-cycle stages/ experimental duration	Effect level biological processes vs pH, CO ₂
Appelhans et al. (2012)	Crustacean	Carcinus maenas	Adults, 10-weeks experiments	No accumulation of extracellular [HCO ₃ ⁻] was measure. Elemental ratios (B/Ca, Mg/Ca and Sr/Ca) in the EPF increased slightly with pH, reflecting an increase growth and calcification rates at higher seawater pH values. The results showed that the highest acidification levels(3500 um) reduce the feeding and growth rates in crabs.
Lagos et al. (2016)	Mollusc	Aegoppecten purpuratus		Shell thickness, weight, and biomass were reduced under low pH (pH 7.7) and increased temperature (18 °C) conditions. At ambient temperature (14 °C) and low pH, scallops showed increased shell dissolution and low growth rates
Thomsen et al. (2013)	Mollusc	Mytilus edulis		Benthic stages of M. edulis tolerate high ambient pCO ₂ when food supply is abundant and that important habitat characteristics such as species interactions and energy availability need to be considered to predict species vulnerability to ocean acidification.

crustaceans, by decreasing calcification rates, or by impacting recruitment, growth and larval survival (Kroeker et al., 2013; Wittmann and Pörtner, 2013; Kroeker et al., 2010; Hendriks et al., 2010; Turley et al., 2011; Turley and Gattuso, 2012). It is also anticipated that the effects associated with ocean acidification could have dramatic consequences this century, potentially even causing extinction of keystone marine species (Dupont et al., 2008). The impact of ocean acidification is a threat to all nations that catch or eat fish, or depend on coral reefs for tourism, storm protection or food. The UK is ranked third among the 25 nations most vulnerable to ocean acidification due to the high level of catch within its exclusive economic zone (EEZ) and the extremely acidified water along its coast predicted by 2050 (Harrould-Koliev et al., 2009).

Major assessments of the economic impact of climate change, for example, Stern (2006) and Nordhaus (2008), however, omit ocean acidification impacts. This, despite ocean acidification potentially having significant financial implications, as the value of marine capture and aquaculture mollusc fisheries produced worldwide amounted to more than US\$ 20 billion in 2010 (FAO, 2012). Other commercial shellfish, such as crustaceans, yielded a worldwide value of around US\$ 31 billion in 2010 (FAO, 2012), and may also be affected by higher levels of acidity, in terms of their development, survival and physiology (Hilmi et al., 2013; Fabry et al., 2008; Kurihara et al., 2008; Arnold et al., 2009), although they are thought to be more tolerant than molluscs. If ocean acidification significantly damages marine habitats, alters marine resource availability, and disrupts ecosystem services, then direct economic costs may occur in addition to indirect impacts, such as potential job losses through declining harvest and fishery revenues from shellfish and their exploited predator species. However, comparatively little research has been undertaken to date regarding the implications of ocean acidification for commercial finfish and shellfish supply to markets (Fabry et al., 2008) except for the studies by Cooley and Doney (2009); Narita et al. (2012); Narita and Rehndanz (2016) and Fernández et al., (2017). There is need to undertake economic studies to estimate the overall welfare impacts resulting from ocean acidification on significant markets such as fisheries, aquaculture and tourism. In this study, we have applied the partial equilibrium (PE) model (Narita et al., 2012) to estimate economy-wide impacts, in addition to using the net present value (NPV) approach (Cooley and Doney, 2009) to quantify the economic losses in revenue from commercial mollusc shellfisheries and aquaculture. Since there are regional variations in the production and consumption of shellfish species across the UK, our analyses consider the potential socio-economic impacts of ocean acidification for each UK devolved administration i.e. England, Scotland, Wales and Northern Ireland.

2. The potential biological impacts of ocean acidification

Increasing atmospheric CO₂ is causing an increase in seawater hydrogen ions (H⁺) concentrations, reducing pH. These changes are quantified under a logarithmic scale, with seawater pH values decreasing as H⁺ increases. Overall, when atmospheric CO₂ dissolves in sea water (H₂O), it forms a series of acid-base equilibria effectively forming carbonic acid (HCO₃). Carbonic acid reacts with carbonate ions (CO₃²⁻) to form the stable bicarbonate ion (HCO₃⁻). These reactions can also reduce carbonate ions, in turn reducing the saturation state of seawater (denoted as Ω = omega). The saturation state of seawater for a mineral is a measure of the potential for the mineral to form or to dissolve. If Ω = less than 1, then carbonate ions are likely to dissolve with implications for marine calcifiers, making it difficult for organisms to build and maintain their skeletons and shells. A wide variety of ecosystem processes and species are thought to be vulnerable to ocean acidification. These include recruitment, growth and larval survival of calcifying organisms at both the molecular and cellular level (Kroeker et al., 2013 and Le Quesne and Pinnegar, 2012), specifically affecting species by decreasing calcification rates (Orr et al., 2005) for organisms

Table 2
Average annual production of shellfish in UK and its devolved administrations (1994–2014).

a)	Volume ('000 tonnes)		Wild capture	Aquaculture	Total shellfish	Shellfish as % of total fisheries
	Molluscs	Crustaceans				
Total UK	52	61	133	30	163	28
England	31	17	61	5	66	54
Wales	5	1	11	11	22	94
Scotland	15	36	55	6	61	16
N. Ireland	2	7	9	8	17	63

b)	Value (£ million)		Wild capture	Aquaculture	Total shellfish	Shellfish as % of total fisheries
	Molluscs	Crustaceans				
Total UK	47	135	203	28	231	40
England	23	34	70	6	76	50
Wales	4	3	11	9	20	81
Scotland	20	88	113	7	120	36
N. Ireland	1	11	13	6	19	73

with a low level of biological control over the calcification process, including molluscs and crustaceans (Kroeker et al., 2010; Hendriks et al., 2010; Turley et al., 2011; Turley and Gattuso, 2012).

Here, a review of relevant (2005–2016) experiments conducted on commercial species (mainly crustaceans and molluscs) was conducted to gain an understanding of the main effects of ocean acidification (see summary Table 1). These studies helped to inform and to calculate the effect size to support further analytical steps during this work. The review only considered studies that dealt with pH changes up to 0.4 pH units, as these are realistic pH scenarios for year 2100. According to these studies, the RCP scenario in which those estimates are realistic is 8.5. Other scenarios, which deal with drastic leaks or carbon sequestration caused by severe local pH changes or natural coastal sites were not considered in this review. We only consider those studies that realistically mimic, via manipulation of carbonate chemistry, the ongoing- and future changes in seawater carbonate chemistry. Any studies that were undertaken during the present century without addition of CO_2^{-3} and or HCO_3^{-} , which had the usage of acid to modify any aspect of the carbonate chemistry, were not deemed to be realistic. We only consider studies that have followed the guidance on good practice for ocean acidification manipulation (see Dickson et al. (2007)).

Findings show that recent experiments are of longer duration (up to 6 months more than previously) but also involve two generations with multiple stressors. A variety of biological responses to ocean acidification have been measured across a range of taxa, and findings show that there is significant variation in the sensitivity of different marine organisms, as higher levels of acidity affect development, survival and physiology (Fabry et al., 2008; Kurihara et al., 2008; Arnold et al., 2009). In addition, there is often considerable variation in the sensitivities of different developmental stages, e.g. between adult and larval phases (Dupont et al., 2008). Some specific commercially important species, particularly shellfish may suffer from reduced growth, impaired reproductive output, or increased mortality (Gazeau et al., 2007; Ries et al., 2009). A study by the US National Oceanic and Atmospheric Administration (NOAA) suggested that a variety of shellfish, ranging from lobsters to oysters, will find it significantly more difficult to grow their skeletons and shells as anthropogenic CO_2 concentrations continue to increase. Emerging data suggests that the number or quality of commercially valuable species, such as aragonite-forming molluscs, could decrease (e.g. Wootton et al., 2008; Hall-Spencer et al., 2008; Gutowska et al., 2008; Seibel, 2007; Fabry et al., 2008; Rosa and Seibel, 2008), as mollusc species suffer from reduced larval survival rates (Talmage and Gobler, 2010), fertilisation success (Fabry et al., 2008) and fitness (Talmage and Gobler, 2010; Michaelidis et al., 2007; Gazeau et al., 2007).

Bivalves may also rely more on the soluble mineral form of CaCO_3 than the mineral used during the adult phase (Weiss et al., 2002), and consequently can suffer extremely high mortality rates (Gosselin and Qian, 1997). Biological responses of molluscs and crustaceans to ocean acidification vary depending on the species, duration of exposure to a particular pH and the bio-lifecycle stage (Table 1). These experiments also show that the larval and juvenile stages of many marine organisms are generally more sensitive to environmental conditions (Kroeker et al., 2013). For example, the malformation of juvenile oyster shells has been observed when the levels of aragonite are below saturation (Cohen and Holcomb, 2009), and the decreased survival of oyster larvae in a commercial hatchery facility was associated with an upwelling of seawater with a decreased pH along the Pacific coasts of Oregon, USA (Barton et al., 2012). Some invertebrates begin the calcification process during the larval or juvenile phases (Kurihara et al., 2008).

Findings show that only a limited number of studies have been conducted on commercially important crustaceans (crabs, lobsters, shrimps, etc.). A reduction in the thermal tolerance of edible crabs (*Cancer pagurus*) has been observed (Metzger et al., 2007), as has a reduction in the carapace mass during the final stage of larval

development in the European lobster, *Homarus gammarus*, which is associated with CO₂-acidified sea water (Arnold et al., 2009). Mobile organisms, such as fish, cephalopods and some crustaceans that can control extracellular pH through active ion transport mechanisms are predicted to be more tolerant to ocean acidification (Gutowska et al., 2008; Pörtner, 2008; Melzner et al., 2009; Whiteley, 2011).

3. The potential socio-economic costs of the impacts of ocean acidification

The socio-economic consequences of ocean acidification, and the economic assessment of the effects of ocean acidification are, in general, sparse in comparison to the research conducted on the potential biological impacts. The shellfish industry is an important part of the UK economy contributing 37% of total landings by value in 2013 (MMO, 2014). Twenty-year landings data shows that between 1994 and 2014, the UK produced 163 000 t of shellfish annually with 133 000 t coming from wild caught shellfish and 30 000 t from shellfish aquaculture (Table 2a). England and Scotland are the highest producers of shellfish with 66 000 t and 61 000 t per year, respectively. In terms of value, the wild capture shellfish is worth £203 million per year and shellfish aquaculture £28 million per year, whilst molluscs and crustaceans together contribute £183 million per year (Table 2b). The UK mollusc wild capture is dominated by scallops (92%) while Nephrops (55%), brown crabs (25%) and lobsters (19%) are the dominant crustacean species landed. Similarly, UK aquaculture is dominated by mussels (95%) and Pacific oysters (4%).

Fig. 1 presents the distribution of commercially exploited shellfish populations in England and Wales. The main offshore species are those that extend into waters shared with other EU states, and include scallops, Nephrops and brown crabs. Indeed, fishing for the scallop, *Pecten maximus*, have at times extended to the 200 m isobath in the Western approaches. Most other species are harvested within the 12 nm fishery limit, whilst cockles, mussels and oyster fisheries, together with all the current aquaculture sites, operate within estuarine areas.

Whilst the UK exports large amounts of shellfish across Europe (including crabs, oysters, mussels, scallops and lobsters), a significant amount is also consumed locally. Each year UK households buy 46 000 t of shellfish comprised of 4000 t of molluscs and 42 000 t of crustaceans (Table 3). The top six species consumed include both cold and warm water prawns, scampi, mussels, crabs and scallops. The gross value added (GVA) based on fishing vessels for which the top species landed

in 2013 was shellfish was estimated to be £124 million (Fig. 2). The value of scallops, Nephrops and lobsters rose between 1990 and 2010, although the value of mussels fell, due to an over-supply through the increasing use of aquaculture, even though demand has risen. Overall, these shellfish production and consumption figures of the UK and its devolved administrations highlight how the impact of ocean acidification would be distributed across the UK.

4. Quantitative assessment

4.1. Data description

The datasets used for this empirical analysis include shellfish landings data (obtained from the Marine Management Organisation (MMO)), aquaculture statistics (obtained from Cefas), and shellfish consumption and gross value-added (GVA) figures (obtained from Seafish). The main shellfish species used in our assessment include cockles, crabs, lobsters, mussels, Nephrops, scallops, shrimps, prawns and whelks. They were included since they have calcium carbonate shells and skeletons that may become more vulnerable to ocean acidification due to concurrent increases in seawater temperature due to the changing climate (Gazeau et al., 2007; Cooley and Doney, 2009; Kroeker et al., 2010; Wood et al., 2008; Haye et al., 2011). We excluded some cephalopods (cuttlefish, squids) as these are thought to be more tolerant (Gutowska et al., 2008; Kurihara et al., 2008; Arnold et al., 2009).

To assess regional variations and volatility in value of different shellfish species due to the existence of ocean acidification effects, the standard deviations of both the quantity and value of landings were used. The instability in quantity and value for wild caught shellfish was assessed using landings data from 1994 to 2014, while for shellfish aquaculture it was based on production figures between 2004 and 2013. Relative vulnerability due to impacts of ocean acidification was calculated as the ratio of total shellfish value over the total value of fish and shellfish landings combined.

4.2. Locally relevant OA projections for the British Isles

In this analysis, we have attempted to make use of locally-relevant model projections for the seas around the British Isles. Blackford and Gilbert (2007) and Artioli et al. (2014) have demonstrated via modelling work the strong seasonality in pH at the sea surface, in the water

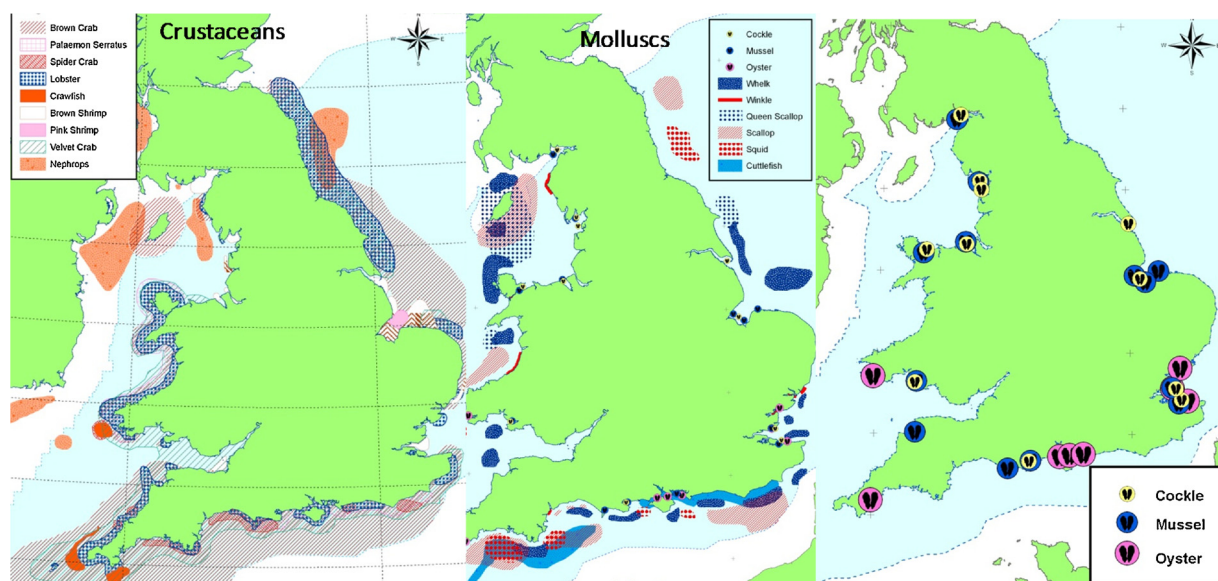


Fig. 1. Distribution of commercially important crustaceans and molluscs species showing the location of shellfish aquaculture sites in England and Wales.

Table 3
Annual average consumption of traded shellfish and shellfish products in UK and the devolved administrations (2010–2015).

a)	Volume ('000 tonnes)				Total shellfish	Shellfish as % of total fisheries
	Molluscs		Crustaceans			
Total UK	4		42		46	13
England	4		38		42	13
Wales	0		3		3	12
Scotland	1		3		4	15

b)	Value (£ million)				Total shellfish	Shellfish as % of total fisheries
	Molluscs		Crustaceans			
Total UK	49		479		527	17
England	45		440		485	17
Wales	3		33		37	16
Scotland	4		38		42	19

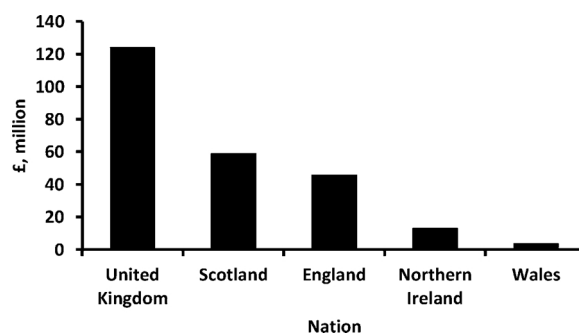


Fig. 2. Total gross value added (GVA) figures for UK and devolved administrations in GBP£ based on fishing vessels for which the top species fished in 2013 was a shellfish species. Values are adjusted to 2015 prices. 'Nation' represents the nation where the vessel is registered.

Table 4
Biogeochemical Scenarios (based on Blackford and Gilbert (2007)).

Scenario	Approx. RCP or SRES equivalent	Atmospheric pCO ₂ (ppm) 2100	pH range 2100	pH mean 2100	Difference from pre-industrial pH
Control (S1)	NA	375	8.1 - 8.3	8.06	0.1
Medium Emissions (S2)	SRES B1, RCP 4.5	550	7.7 - 8.3	7.82	0.35
High Emissions (S3)	SRES A1F1, RCP 8.5	1000	7.6 - 8.1	7.67	0.49

column and at the seafloor. This work indicates a spatial and temporal heterogeneity linked to local hydrodynamics and biological processes (Artoli et al., 2014). The use of future projections has been done considering a high (A1B and RCP 8.5) emission scenarios: with conditions of seasonal under-saturation of aragonite projected for ~30% of the bottom waters of the North Sea by 2100 (Artoli et al., 2014). These details are important especially in the coastal strip where most shellfish production occurs. Consequently, we have taken the mean value in each instance (Table 4a). In theory, it would be desirable to match fine-scale site-specific pH or pCO₂ projections with the molluscs and crustaceans present at individual fishing grounds or aquaculture sites. However, this level of detailed analysis is currently unfeasible, given the available scientific knowledge. It should be noted that we assume the same pH values in all four UK nations/territories (England, Wales, Scotland, Northern Ireland), even though we are aware from recent observations (Ostle et al., 2016) that pH can vary between 7.9 and 8.1 at different sites around the UK coast. Preliminary modelling data by UKOA researchers indicate that much of the North Sea seafloor is likely to become seasonally under-saturated (during late winter/early spring) regarding aragonite by 2100 under high CO₂ emission scenarios (Artoli et al., 2014).

4.3. Biological assumptions – effect size

For each of the three biogeochemical scenarios we have needed to derive an understanding of how the main shellfish species present in the UK might be impacted. To achieve this, we used the global experimental literature on commercial shellfish species (Table 1) and collated information on 'effect size' from 11 studies that covered relevant life stages and responses. The data extraction was concentrated in the response of commercial species and/or processes to experimental ocean acidification treatments and the corresponding values of the control treatments. We use the experimental treatments with the medium and highest pH used in the experimental set-up. A total of 11 studies were included in this analysis following the methodology adopted by Ramajo

Table 5

Effect sizes for molluscs and crustaceans calculated based on the biological assumptions for medium and high emission scenarios.

Scenario	pH median 2100	Effect size - Crustaceans	Effect size - Molluscs
Control	8.06	0	0
Medium Emissions	7.82	0.3	0.4
High Emissions	7.67	0.6	0.8

et al. (2016) and Kroeker et al. (2013) and Ramajo et al. (2016). The log-transformed response ratio (LnRR), which is the ratio of the mean effects in the acidification treatment to the mean effect in a control group (Hedges et al., 1999) was calculated across studies. A log-transformed response ratio of zero is interpreted as the experimental treatment having no effect on the response variable, while a positive value indicates a positive effect and a negative value indicates a negative effect. We have divided the species into molluscs and crustaceans, as the various meta-analyses that have been completed in recent years by Kroeker et al. (2013); Hendriks et al. (2010) and Kroeker et al. (2010) have all indicated that crustaceans are more robust to simulated pH changes than are molluscs (bivalves and gastropods). The effect size (Table 5) at different pH values were used to calculate anticipated financial losses in 2100.

4.4. Estimating potential harvest losses due to ocean acidification

To estimate the potential harvest losses of UK shellfish due to ocean acidification, the net present value (NPV) approach (Cooley and Doney, 2009) was used. The NPV approach quantifies the direct economic costs of potential ocean acidification damage in the present in contrast to some future costs it will have. It therefore compares the ocean acidification costs during shellfish production against the counterfactual baseline production value with no acidification over a period. Because of the time value of money i.e. money in the present is worth more than the same amount in the future, a social discount rate is used. Here, we have assumed a constant price in sterling pounds, ignoring price changes due to supply reductions because of ocean acidification, hence no change in the proportions of shellfish catch over time (Cooley and Doney, 2009). We have used 3.5% social discount rate as recommended by the UK Treasury (HM Treasury, 2003) for forward projection. We have also assumed that the onset of ocean acidification affects both wild-capture shellfish and those derived from aquaculture equally, and that the rate of harvest loss of shellfish is proportional to the decrease in calcification rate due to ocean acidification, in line with assumptions made in Cooley and Doney (2009); Narita et al. (2012) and Narita and Rehdanz (2016). Thus, the aggregate economic losses in provisioning services for 2100 were calculated at 2013 prices together with the emission scenarios and the biological responses (effect sizes) of molluscs and crustaceans. Further work conducted on the potential impacts of ocean acidification and warming on future fisheries catches, revenue and employment in the UK fishing industry under different CO₂ emission scenarios showed that species were likely to be more affected by ocean acidification and warming combined, than by ocean warming alone (Fernandes et al., 2017). This work found that projected standing stock biomasses could decrease by 10–60%; losses in revenue could decrease by 1–21%; and losses in relevant employment (fisheries and associated industries) could decrease by 3–20% during 2020 – 2050 (Fernandes et al., 2017). Given the uncertainty surrounding the biological responses to ocean acidification, a sensitivity analysis was carried out to assess how the economic figures are resilient to uncertainty in the estimates of the biological impact. Different effect sizes were therefore explored under each of the emissions scenarios including i) for molluscs (0.1–0.4 for medium emissions, and 0.5–0.8 for high emissions), and ii) crustaceans (0.1–0.3 for medium emissions and 0.4–0.6 for high

emissions). The results are presented as a range from low to high based on the effect size used.

The potential direct costs of shellfish loss due to ocean acidification would also affect macroeconomic elements (such as output, income and employment), and therefore we applied a partial-equilibrium (PE) analysis to assess the wider impacts of ocean acidification on molluscs and crustaceans (Narita et al., 2012; Narita and Rehdanz, 2016). The PE framework measures the welfare losses due to reduced production and consumption, and the welfare effects of price increase under reduced supply due to ocean acidification. The PE model has an advantage over the NPV approach as it reflects the impact of price increases resulting from supply reduction following ocean acidification impacts with market commodity demand changes and income and population growth up to 2100. It measures the exogenous shock thereby capturing the welfare losses subject to the slopes of the supply and demand curves (Narita et al., 2012). Our parameter levels for the demand and supply elasticity for UK wild-capture and aquaculture were based on empirical estimates using the shellfish landings and consumption figures. Linear regressions were computed using the landings data (supply) and consumption figures (demand) over time and the coefficients used to model changes in demand and supply for shellfish. The regressions were conducted with data pooled for the whole UK, and separately for each UK devolved administration. Based on the emission scenarios and the biological responses of both molluscs and crustaceans, we used the effect sizes to estimate potential losses to producer and consumer surplus, and net total loss for the economy due to ocean acidification.

5. Results

5.1. Quantity and price volatility

The quantity and value of crustaceans produced and consumed in the UK shows higher volatility than for molluscs (Table 6). Twenty-year production figures show that instability is highest for scallops based on the volume produced but highest for Nephrops based on value of landings. Given that scallops and Nephrops are the top shellfish species produced, the volatility in volume and value implies that potentially the UK is at a high level of risk from ocean acidification. Similarly, the proportion of wild-caught shellfish compared to total fisheries (fin-fish + shellfish) produced by the UK per year ranged from 50% in Wales to 93% in England showing that the shellfish sector is commercially significant in all regions (Table 7). These data reveal that England (50%) and Wales (43%) are more vulnerable to the effects of ocean acidification from molluscan production while Northern Ireland (79%) and Scotland (66%) are more vulnerable from the production of crustaceans. Results show that out of the four devolved administrations, Wales will potentially experience the highest ocean acidification impacts as 94% of its fisheries production is shellfish. Assuming the onset of ocean acidification affects both wild-caught shellfish and those

Table 6

Volatility in production of shellfish species measured as standard deviation of value and quantity during 1994–2014.

Species	Volume ('000 tonnes)	Species	Value (£ million)
Nephrops	5.4	Nephrops	22.7
Scallops	10.7	Scallops	13.3
Lobsters	0.8	Lobsters	8.9
Crabs	3.5	Crabs	6.8
Cockles	8.0	Cockles	3.9
Mussels	5.1	Mussels	1.5
Shrimps and Prawns	0.7	Shrimps and Prawns	1.0
Crustaceans average	7.4	Crustaceans average	36.7
Molluscs average	6.0	Molluscs average	12.2
Shellfish aquaculture	4.1	Shellfish aquaculture	8.3

Table 7

Vulnerability (%) to production of molluscs, crustacea and aquaculture based on the average (1994 – 2014) volume of shellfish produced by UK and its devolved administrations.

	UK	England	Wales	Scotland	NI
Molluscs	39%	50%	43%	28%	18%
Crustaceans	46%	28%	10%	66%	79%
Wild capture	81%	93%	50%	90%	51%
Aquaculture	19%	7%	50%	10%	49%
Shellfish fisheries	28%	54%	94%	16%	63%
Gross value added (2013)		48%	37%	10%	3%

derived from aquaculture equally, and that the rate of harvest loss of shellfish is proportional to the decrease in calcification rate due to ocean acidification, then overall ocean acidification will have considerable impacts on the UK shellfish industry.

5.2. Economy-wide implications of ocean acidification

In 2013, landings by UK vessels into UK ports had a value of £68 million for molluscs and £157 million for crustaceans (MMO, 2014). Adjusted to present day values using a 3.5% discount rate and integrated up until 2100, the net present value (NPV) for molluscs is £1847 million and £4265 million for crustaceans. This assumes there are no changes to the current economic and ecological conditions. While the anticipated future revenue losses are worth less than losses today because of the compounding effects of interest and capital return rates, data shows that the economic losses due to ocean acidification could be substantial. They range from £739 to £1478 million for molluscs and £1279 to £2559 for crustaceans depending on the emission scenario and biological response (Table 8). Using locally relevant ocean acidification projections for the British Isles of atmospheric pCO₂ of 700 ppm in 2100, pH range of 7.7–8.3 and pH median of 7.82 to represent medium emissions scenario while atmospheric pCO₂ of 1000 ppm in 2100, pH range of 7.6–8.1 and pH median of 7.67 for high emissions scenario shows that vessel revenues will decrease by 14–28%. However, these losses will not be spread evenly across the UK devolved regions. Wales will experience the highest potential losses due to molluscan production of 17–34% while Scotland the highest potential loss

Table 8

Time integrated NPV by 2100 of the potential economic losses to UK shellfish wild capture and aquaculture under medium and high CO₂ emission based on local projections of atmospheric pCO₂ and effect sizes from biological assumptions for molluscs and crustaceans. NPV are in millions based on 2013 GB pounds sterling. The low and high end of each range is based on different effects sizes to show how sensitive the economic figures are to changes in biological impact.

Region	Scenario	Molluscs	Crustaceans	Wild capture	Aquaculture	All shellfish (wild + aquaculture)
UK	NPV with no impact of CO ₂	1847	4265	6995	1305	8301
	Medium Emissions	185–739	426–1279	700–2448	131–457	830–2905
	High Emissions	923–1478	1706–2559	2798–4897	522–914	3320–5810
	% loss from fishery NPV	10.6–21.1	18.3–36.6	11.8–23.6	2.2–4.3	14.0–28.0
England	NPV with no impact of CO ₂	749	1291	2572	466	3039
	Medium Emissions	75–300	129–387	257–900	47–163	304–1064
	High Emissions	374–599	516–775	1029–1801	187–326	1215–2127
	% loss from fishery NPV	11.6–23.3	15.1–30.1	13.8–27.7	2.5–5.0	16.3–32.7
Scotland	NPV with no impact of CO ₂	721	2451	3394	243	3637
	Medium Emissions	72–288	245–735	339–1188	24–85	364–1273
	High Emissions	360–576	980–1470	1358–2376	97–170	1455–2546
	% loss from fishery NPV	8.4–17.0	21.7–43.3	10.0–20.0	0.7–1.4	10.1–21.4
Wales	NPV with no impact of CO ₂	135	70	318	430	748
	Medium Emissions	14–54	7–21	32–111	43–151	75–262
	High Emissions	67–108	28–42	127–223	172–301	299–524
	% loss from fishery NPV	17.0–34.1	6.6–13.3	12.6–25.3	17.1–34.2	29.7–59.4
NI	NPV with no impact of CO ₂	76	426	508	166	673
	Medium Emissions	8–30	43–128	51–178	17–58	67–236
	High Emissions	8–61	170–256	203–355	83–116	269–471
	% loss from fishery NPV	6.0–12.0	25.2–50.3	12.1–24.3	4.0–7.9	16.1–32.2

Table 9

Losses (mean \pm standard deviation) of consumer and producer surpluses, and net total loss for the economy due to ocean acidification on molluscan and crustacean production in UK and devolved administration.

		Loss of producer surplus		Loss of consumer surplus		Net total loss for the economy	
		Mean	SD	Mean	SD	Mean	SD
UK	All shellfish	8.4	5.5	46.3	24.0	38.0	29.5
	Crustaceans	33.4	32.6	54.4	14.5	87.9	47.1
	Molluscs	13.7	9.3	9.1	0.9	22.9	10.2
England	All shellfish	5.4	11.3	35.0	14.0	40.5	25.3
	Crustaceans	22.4	11.5	8.0	2.8	30.4	14.3
	Molluscs	0.1	0.7	4.2	2.6	4.3	3.4
Wales	All shellfish	1.1	1.2	2.9	1.2	4.0	2.4
	Crustaceans	2.0	1.4	2.5	1.0	4.5	2.4
	Molluscs	0.0	0.1	0.4	0.3	0.4	0.3
Scotland	All shellfish	0.7	0.6	2.7	2.1	3.4	2.7
	Crustaceans	20.1	12.0	7.0	3.2	27.1	15.2
	Molluscs	0.6	0.7	2.1	1.2	2.6	1.9
NI	All shellfish	0.3	0.7	2.7	1.2	3.0	1.9
	Crustaceans	0.6	0.6	5.2	2.3	4.6	2.9
	Molluscs	0.8	0.5	0.6	0.3	1.3	0.8

due to crustacean harvest of 22–43% of wild capture shellfish NPV. Overall, Wales will be the most heavily impacted devolved administration losing between 30–59% of total shellfish NPV (Table 8).

Table 9 shows the overall potential loss to producer and consumer surplus and the net total loss for the economy to shellfish production due to ocean acidification in the UK and its devolved administrations. While crustaceans are expected to show a much greater tolerance to ocean acidification than molluscs, the high volume of Nephrops and brown crabs produced and consumed in the UK mean that total economic losses from ocean acidification will be much higher than from molluscs. Findings show average net total loss to the economy of £88 \pm 47 million from crustacean compared to £38 \pm 29 million for molluscan production and consumption. Of the four devolved administrations, England shows the highest cumulative loss to GDP from shellfish production and consumption due to ocean acidification. Apart from the total economic loss from crustacean production in Scotland

that is predicted to be considerably higher, losses to producer and consumer surplus for both molluscs and crustaceans show roughly even distribution in Wales and Northern Ireland.

6. Discussion

The aim of this paper was to evaluate the potential costs of ocean acidification to the UK and its devolved administrations by using a combination of the partial equilibrium (PE) model and the net present value (NPV) approach. The NPV approach which included a discount rate of 3.5% and was integrated until 2100, demonstrated that the direct potential losses due to reduced shellfish production in the UK would range from 14% to 28% of fishery NPV. This equates to potential annual economic costs of between £3 and £6 billion of the UK's GDP in 2013, for medium and high emission scenarios. Although this approach is simple to apply in terms of direct value losses, it assumes that all the variables are constant and so the gradual upward trend in GDP (income effect) to 2100 is ignored.

The PE approach, on the other hand, is more realistic, although uncertainty remains as it is projected forward to the year 2100. Results using the PE model show that the total loss to the UK economy from shellfish production and consumption range from £23 - £88 million. The results from both the direct valuation and predicted estimate for the economic losses due to ocean acidification on shellfish harvest indicate that there are regional variations due to different patterns of shellfish wild-capture and aquaculture, and the exploitation of species with differing sensitivities to ocean acidification. In the short- and medium-term, Wales and England are more susceptible while over the long-term all the nations (including Scotland and Northern Ireland) will be susceptible to the effects of ocean acidification. This is because a substantial industry surrounds the catching, processing, transport and resale of shellfish in each nation. In relative terms, the regional impacts in Northern Ireland and Wales will probably be greater than in England and Scotland as these nations rely more on shellfish production. The scale and speed of expansion of the shellfish aquaculture sector in England and Wales (29,385 mollusc production sites) compared to 323 in Scotland and 74 in Northern Ireland also mean that the impacts are likely to be unevenly distributed across the UK. Scotland however, may be more vulnerable to job losses than the other regions, due to its high reliance on fishing and fish processing by the coastal communities (FAIRSE, 2002).

The approach used in this study offers a proof of concept where the NPV method indicates the potential direct losses in shellfish production due to ocean acidification while the PE approach reflects losses to per capita incomes and economy-wide welfare losses from ocean acidification. These evaluation methods are constrained by the availability of scientific assessments on the biological impact of ocean acidification during longer-term experiments for different life-stages, as well as food-web effects on fisheries. However, the variation in calcification response to ocean acidification amongst different polymorphs of calcium carbonate with crustaceans is acknowledged in Kroeker et al. (2011) and also Andersson and Mackenzie (2011), as crustaceans (e.g. crabs, lobsters, shrimps) are high Mg-calcite skeletal organisms with a very complex mineralogy, and the observed calcification response may flaw the meta-analysis of the effect of ocean acidification on calcification categorized by carbonate mineralogy (Andersson and Mackenzie, 2011).

Addressing the problem of ocean acidification with the aim of preserving commercially valuable shellfish resources will require regional, national or international solutions to be sought, including a reduction in atmospheric CO₂ emissions (mitigation) and possibly a shift in focus to species that are less vulnerable to ocean acidification effects (adaptation). As well as ocean acidification, there will be changes in other environmental variables because of anthropogenic climate change, including ocean warming, incidents of hypoxia, changes in salinity, physical disturbance, and changes in ocean mixing

and stratification (Pörtner, 2008). Some local-scale strategies could be put into place to directly combat ocean acidification in seawater, such as by increasing alkalinity. However, these geo-engineering methods are likely to be expensive and energy intensive, yielding only a small or local benefit. Other strategies, such as updating fishery management plans (reducing the permissible levels of exploitation) to include acidification effects, are less costly and can be regionally tailored as required to accommodate biological, economic and social variations between regions (Doney et al., 2009). It is worth noting that some species could also benefit (directly or indirectly) from ocean acidification and this could further stimulate socio-economic adaptive response.

Inter-regional policies must begin with monitoring of: (i) the progress of ocean acidification along with coastal and open ocean seawater chemistry; (ii) commercial and key species' responses to decreased pH and elevated CO₂ levels, and the sensitivity of molluscs, crustaceans, and finfish larvae, juveniles, and adults to changing seawater chemistry; (iii) quantifying indirect effects from prey losses for fisheries dominated by predatory finfish, the relative effects of prey switching, benthic and habitat degradations, and overall biomass reduction; and (iv) socio-economic impacts, adaptation, and mitigation to declining fishery production. The likelihood of complex secondary effects resulting from ocean acidification emphasises the need for developing and using ecosystem-based management models (Arnold et al., 2009). Further research is required which simultaneously addresses both elevated CO₂ levels and temperature changes across animal groups and phyla over the longer term. This should address effects on reproduction, growth, fitness and survival, especially in lower trophic level marine invertebrates. Future research might also focus on the identification of species and habitats which may have more capacity to acclimate to future ocean chemistry changes and to mitigate potential impacts.

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References

- Agnalt, A., Grefsrud, E., Faresteit, E., Larsen, M., Keulder, F., 2013. Deformities in larvae and juvenile European lobster (*Homarus gammarus*) exposed to lower pH at two different temperatures. *Biogeosciences* 10, 7883–7895.
- Andersson, A., Mackenzie, F., 2011. Technical comment on Kroeker et al., Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* 14, 840.
- Appelhans, Y.S., Thomsen, J., Pansch, C., Melzner, F., Wahl, M., 2012. Sour times: sea-water acidification effects on growth, feeding behaviour and acid-base status of *Asterias rubens* and *Carcinus maenas*. *Mar. Ecol. Prog. Ser.* 459, 85–98.
- Arnold, K., Findlay, H., Spicer, J., Boothroyd, D., 2009. Effect of CO₂-related acidification on aspects of the larval development of the European lobster, *Homarus gammarus* (L.). *Biogeosciences* 6, 1747–1754.
- Artoli, Y., Blackford, J.C., Nondal, G., Bellerby, R.G.J., Wakelin, S.L., Holt, J.T., Butenschön, M., Allen, J.I., 2014. Heterogeneity of impacts of high CO₂ on the North Western European shelf. *Biogeosciences* 11, 601–612. <http://dx.doi.org/10.5194/bg-11-601-2014>.
- Barros, P., Sobral, P., Range, L., Chicharro, D., 2013. Effects of sea-water acidification on fertilization and larval development of the oyster *Crassostrea gigas*. *J. Exp. Mar. Biol. Ecol.* 440, 200–206.
- Barton, A., Hales, B., Waldbusser, G., Langdon, C., Feely, R., 2012. The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: implications for near-term ocean acidification effects. *Limn. Oceanogr.* 57, 698–710.
- Berge, J.A., Bjerkeng, B., Pettersen, O., Schaanning, M.T., Øxnevad, S., 2006. Effects of increased sea water concentrations of CO₂ on growth of the bivalve *Mytilus edulis* L. *Chemosphere* 62, 681–687. <http://dx.doi.org/10.1016/j.chemosphere.2005.04.111>.
- Blackford, J., Gilbert, F., 2007. pH variability and CO₂ induced acidification in the North Sea. *J. Mar. Syst.* 64, 229–241.
- Bressan, M., Chinellato, A., Munari, M., Matozzo, V., Mancini, A., Marčeta, T., Finos, L., Moro, I., Pastore, P., Badocco, D., Marin, M., 2014. Does seawater acidification affect survival, growth and shell integrity in bivalve juveniles? *Mar. Environ. Res.* 99, 136–148.

- Caldeira, K., Wickett, M., 2003. Anthropogenic carbon and ocean pH. *Nature* 425, 365.
- Clements, J., Hunt, H., 2014. Influence of sediment acidification and water flow on sediment acceptance and dispersal of juvenile soft-shell clams (*Mya arenaria* L.). *J. Exp. Mar. Biol. Ecol.* 453, 62–69.
- Cohen, A., Holcomb, M., 2009. Why corals care about ocean acidification: uncovering the mechanism. *Oceanogr. Mar. Biol.* 22, 118–127.
- Cooley, S., Doney, S., 2009. Anticipating ocean acidification's economic consequences for commercial fisheries. *Environ. Res. Lett.* 4, 024007. <http://dx.doi.org/10.1088/1748-9326/4/2/024007>.
- Dickson, A., Sabine, C., Christian, J., 2007. Guide to best practices for ocean CO₂ measurements. *PICES Special Publ.* 3, 191.
- Dineshram, R., Wong, K., Xiao, S., Yu, Z., Qian, P., Thiyagarajan, V., 2012. Analysis of Pacific oyster larval proteome and its response to high-CO₂. *Mar. Pollut. Bull.* 64, 2160–2167.
- Doney, S., Fabry, V., Feely, R., Kleypas, J., 2009. Ocean acidification: the other CO₂ problem. *Ann. Rev. Mar. Sci.* 1, 169–192.
- Donohue, P., Calosi, P., Bates, A., Laverock, B., Rastrick, S., Mark, F., Strobel, A., Widdicombe, S., 2012. Impact of exposure to elevated pCO₂ on the physiology and behaviour of an important ecosystem engineer, the burrowing shrimp *Upogebia deltaura*. *Aqua Biol.* 15, 73–86.
- Duarte, C., Navarro, J., Acuña, K., Torres, R., Manríquez, P., Lardies, M., Vargas, C., Lagos, N., Aguilera, V., 2014. Intraspecific variability in the response of the edible Mussel *Mytilus chilensis* (Hupe) to ocean acidification. *Estuaries Coasts* 38. <http://dx.doi.org/10.1007/s12237-014-9845-y>.
- Dupont, S., Havenhand, J., Thorndyke, W., Peck, L., Thorndyke, M., 2008. Near-future level of CO₂-driven ocean acidification radically affects larval survival and development in the brittlestar *Ophiotrix fragilis*. *Mar. Ecol. Prog. Ser.* 373, 285–294.
- Fabry, V., Seibel, B., Feely, R., Orr, J., 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.* 65, 414–432.
- FAIRSE (Fraser of Allander Institute for Research on the Scottish Economy), 2002. Input-output Multiplier Study of the UK and Scottish Fish Catching and Fish Processing Sectors. University of Strathclyde.
- FAO, 2012. Yearbook 2010: Fishery and Aquaculture Statistics. Rome.
- Fernandes, J.A., Papathanasopoulou, E., Hattam, C., Queirós, A.M., Cheung, W.W., Yool, A., Artioli, Y., Pope, E.C., Flynn, K.J., Merino, G., Calosi, P., 2017. Estimating the ecological, economic and social impacts of ocean acidification and warming on UK fisheries. *Fish Fisheries* 18, 389–411. <http://dx.doi.org/10.1111/faf.12183>.
- Fitzer, S., Cusack, M., Phoenix, K., Kamenos, N., 2014. Ocean acidification reduces the crystallographic control in juvenile mussel shells. *J. Struct. Biol.* 188, 39–45.
- Gazeau, F., Gattuso, J., Dawber, C., Pronker, A., Peene, F., Peene, J., Heip, C., Middelburg, J., 2010. Effect of ocean acidification on the early life stages of the blue mussel *Mytilus edulis*. *Biogeosciences* 7, 2051–2060.
- Gazeau, F., Quiblier, C., Jansen, J., Gattuso, J., Middelburg, J., Heip, C., 2007. Impact of elevated CO₂ on shellfish calcification. *Geophys. Res. Lett.* 34, L07603.
- Gosselin, L., Qian, P., 1997. Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 146, 265–282.
- Götze, S., Matoo, O., Benias, E., Saborowski, R., Sokolova, I., 2014. Interactive effects of CO₂ and trace metals on the proteasome activity and cellular stress response of marine bivalves *Crassostrea virginica* and *Mercenaria mercenaria*. *Aqua Toxicol.* 149, 65–82.
- Gutowka, M.A., Pörtner, H.O., Melzner, F., 2008. Growth and calcification in the cephalopod *Sepia officinalis* under elevated seawater pCO₂. *Mar. Ecol. Prog. Ser.* 373, 303–309.
- Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D., Buia, M.C., 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454, 96–99.
- Hammer, K.M., Pedersen, S., Størseth, T., 2012. Elevated seawater levels of CO₂ change the metabolic fingerprint of tissues and hemolymph from the green shore crab *Carcinus maenas*. *Comp. Biochem. Physiol. Part D Genom. Proteom.* 7, 292–302.
- Harrould-Kolieb, E., Hirschfeld, M., Brosius, A., 2009. Major emitters among hardest hit by OA: an analysis of the impacts of acidification on the countries of the world. *Oceana Rep.* 11.
- Havenhand, J., Schlegel, P., 2009. Near-future levels of ocean acidification do not affect sperm motility and fertilization kinetics in the oyster *Crassostrea gigas*. *Biogeosciences* 6, 3009–3015.
- Haye, K.L., Spicer, J., Widdicombe, S., Briffa, M., 2011. Reduced sea water pH disrupts resource assessment and decision making in the hermit crab *Pagurus bernhardus*. *Anim. Behav.* 82, 495–501.
- Hedges, L.V., Gurevitch, J., Curtis, P., 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80, 1150–1156.
- Heinemann, A., Fietzke, J., Melzner, F., Böhm, F., Thomsen, J., Garbe-Schönberg, C., Eisenhauer, A., 2012. Conditions of *Mytilus edulis* extracellular body fluids and shell composition in a pH-treatment experiment: acid-base status, trace elements and d11B. *Geochim. Geophys. Geosyst.* 13, Q01005. <http://dx.doi.org/10.1029/2011GC003790>.
- Hendriks, I.E., Duarte, C.M., Alvarez, M., 2010. Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuar. Coast. Shelf Sci.* 86, 157–164.
- Hernroth, B., Krång, A., Baden, S., 2015. Bacteriostatic suppression in Norway lobster (*Nephrops norvegicus*) exposed to manganese or hypoxia under pressure of ocean acidification. *Aquat. Toxicol.* 159, 217–224.
- Hernroth, B., Sköld, H.N., Wiklander, K., Jutfelt, F., Baden, S., 2012. Simulated climate change causes immune suppression and protein damage in the crustacean *Nephrops norvegicus*. *Fish Shellfish Immunol.* 33, 1095–1101.
- Hilmi, N., Allemand, D., Dupont, S., Safa, A., Haraldsson, G., Nunes, P.-D., Moore, C., Hattam, C., Reynaud, S., Hall-Spencer, J., Fine, M., Turley, C., Jeffree, R., Orr, J., Munday, P., Cooley, S., 2013. Towards improved socio-economic assessments of ocean acidification's impacts. *Mar. Biol.* 160, 1773–1787.
- HM Treasury, 2003. The Green Book: Appraisal and Evaluation in Central Government. IPCC, 2001. In: Houghton, J.T. (Ed.), *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- Ivanina, A.V., Dickinson, G.H., Matoo, O.B., Bagwe, Rita, Dickinson, A., Benias, E., Sokolova, I.A., 2013. Interactive effects of elevated temperature and CO₂ levels on oyster metabolism and biomineralization of marine bivalves *Crassostrea virginica* and *Mercenaria mercenaria*. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 166, 101–111.
- Klok, C., Wijsman, J., Kaag, K., Foekema, E., 2014. Effects of CO₂ enrichment on cockle shell growth interpreted with a dynamic energy budget model. *J. Sea Res.* 94, 111–116.
- Kroeker, K.J., Kordas, R.L., Ryan, N., Crim, R.N., Singh, G.G., 2011. Response to technical comment on 'meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms'. *Ecol. Lett.* 14, E1–E2.
- Kroeker, K.J., Kordas, R.L., Crim, R.N., Hendriks, I.E., Ramajo, L., Singh, G.G., Duarte, C., Gattuso, J.P., 2013. Impacts of ocean acidification on marine biota: quantifying variation in sensitivity among organisms and life stages and at elevated temperature. *Glob. Change Biol.* 19, 1884–1896.
- Kroeker, K.J., Kordas, R.L., Crim, R.N., Singh, G.G., 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* 13, 1419–1434.
- Kurihara, H., Matsui, M., Furukawa, H., Hayashi, M., Ishimatsu, A., 2008. Long-term effects of predicted future seawater CO₂ conditions on the survival and growth of the marine shrimp *Palaemon pacificus*. *J. Exp. Mar. Biol. Ecol.* 367, 41–46.
- Lagos, N.A., Benítez, S., Duarte, C., Lardies, M.A., Broitman, B.R., Tapia, C., Tapia, P., Widdicombe, S., Vargas, C., 2016. Effects of temperature and ocean acidification on shell characteristics of *Argopecten purpuratus*: implications for scallop aquaculture in an upwelling-influenced area. *Aquacult. Environ. Interact.* 8, 357–370. <http://dx.doi.org/10.1007/s10334-016-00183>.
- Lannig, G., Eilers, S., Pörtner, H.-O., Sokolova, I.M., Bock, C., 2010. Impact of ocean acidification on energy metabolism of oyster, *Crassostrea gigas* - changes in metabolic pathways and thermal response. *Mar. Drugs* 8, 2318–2339.
- Lardies, M.A., Arias, M.B., Poupin, M.J., Manríquez, P.H., Torres, R., Vargas, C.A., Navarro, J.M., Lagos, N.A., 2014. Differential response to ocean acidification in physiological traits of *Concholepa* populations. *J. Sea Res.* 90, 127–134. <http://dx.doi.org/10.1016/j.seares.2014.03.010>.
- Le Quesne, W.J.F., Pinnegar, J.K., 2012. The potential impacts of ocean acidification: scaling from physiology to fisheries. *Fish Fisheries* 13, 333–344. <http://dx.doi.org/10.1111/j.1467-2979.2011.00423.x>.
- Long, W.C., Swiney, K.M., Foy, R.J., 2013. Effects of ocean acidification on the embryos and larvae of red king crab, *Paralithodes camtschaticus*. *Mar. Pollut. Bull.* 69, 38–47.
- Manríquez, P.H., Jara, M.E., Mardones, M.L., Torres, R., et al., 2014. Ocean acidification affects predator avoidance behaviour but not prey detection in the early ontogeny of a keystone species. *Mar. Ecol. Prog. Ser.* 502, 157–167. <http://dx.doi.org/10.3354/meps10703>.
- Melzner, F., Gutowka, M.A., Langenbuch, M., Dupont, S., Lucassen, M., Thorndyke, M.C., Bleich, M., Pörtner, H.O., 2009. Physiological basis for high CO₂ tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences* 6, 2313–2331.
- Metzger, R., Sartoris, F.J., Langenbuch, M., Pörtner, H.O., 2007. Influence of elevated CO₂ concentrations on thermal tolerance of the edible crab *Cancer pagurus*. *J. Therm. Biol.* 32, 144–151.
- Michaelidis, B., Spring, A., Pörtner, H.O., 2007. Effects of long-term acclimation to environmental hypercapnia on extracellular acid–base status and metabolic capacity in Mediterranean fish *Sparus aurata*. *Mar. Biol. (Berl.)* 150, 1417–1429.
- MMO, 2014. UK Sea Fisheries Statistics 2014. National Statistics / Department for Environment, Food & Rural Affairs, London 138 pp.
- Narita, D., Rehndanz, K., 2016. Economic impact of ocean acidification on shellfish production in Europe. *J. Environ. Plan. Manage.* 1–19. <http://dx.doi.org/10.1080/09640568.2016.1162705>.
- Narita, D., Rehndanz, K., Tol, R.S.J., 2012. Economic costs of ocean acidification: a look into the impacts on shellfish production. *Clim. Change* 113, 1049–1063. <http://dx.doi.org/10.1007/s10584-011-0383-3>.
- Navarro, J.M., Torres, R., Acuña, K., Duarte, C., Manríquez, P.H., Lardies, M., Lagos, N.A., Vargas, C., Aguilera, V., 2013. Impact of medium-term exposure to elevated pCO₂ levels on the physiological energetics of the mussel *Mytilus chilensis*. *Chemosphere* 90, 1242–1248.
- Nordhaus, W., 2008. *A Question of Balance: Weighing the Options on Global Warming Policies*. Yale University Press, New Haven, CT.
- Omera, B.M., Ivanina, A.I., Ullstad, C., Benias, E., Sokolova, I.M., 2013. Interactive effects of elevated temperature and CO₂ levels on metabolism and oxidative stress in two common marine bivalves (*Crassostrea virginica* and *Mercenaria mercenaria*). *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 164, 545–553.
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Kopp, R.M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G.-K., Rodgers, K.B., Sabine, C.L., Sarmiento, J.L., Schlitzer, R., Slater, R.D., Totterdell, I.J., Weirig, M.-F., Yamanaka, Y., Yool, A., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437, 681–686.
- Ostle, C., Williamson, P., Artioli, Y., Bakker, D.C.E., Birchenough, S., Davis, C.E., Dye, S., Edwards, M., Findlay, H.S., Greenwood, N., Hartman, S., Humphreys, M.P., Jickells, T., Johnson, M., Landschützer, P., Parker, R., Pearce, D., Pinnegar, J., Robinson, C., Schuster, U., Silburn, B., Thomas, R., Wakelin, S., Walsham, P., Watson, A.J., 2016. Carbon Dioxide and Ocean Acidification Observations in UK Waters: Synthesis Report

- With a Focus on 2010–2015.
- Pearson, P.N., Palmer, M.R., 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* 406, 695–699.
- Pörtner, H.O., 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Mar. Ecol. Prog. Ser.* 373, 203–217.
- Ramajo, L., Pérez-León, E., Hendriks, I.E., Marbà, N., Krause-Jensen, D., Sejr, M.K., Blicher, M.E., Lagos, N.A., Olsen, Y.S., Duarte, C.M., 2016. Food supply confers calcifiers resistance to ocean acidification. *Nat. Sci. Rep.* 6, 19374. <http://dx.doi.org/10.1038/srep19374>.
- Range, P., Chicharro, M.A., Ben-Hamadou, R., Piló, D., Matias, D., Joaquim, S., Oliveira, A.P., Chicharro, L., 2011. Calcification, growth and mortality of juvenile clams *Ruditapes decussatus* under increased pCO₂ and reduced pH: variable responses to ocean acidification at local scales? *J. Exp. Mar. Biol. Ecol.* 396, 177–184.
- Richards, R.G., Davidson, A.T., Meynecke, J.O., Beattie, K., Hernaman, V., Lynam, T., van Putten, I., 2015. Effects and mitigations of ocean acidification on wild and aquaculture scallop and prawn fisheries in Queensland, Australia. *Fish. Res.* 161, 42–56.
- Ries, J.B., Cohen, A.L., McCorkle, D.C., 2009. Marine calcifiers exhibit mixed responses to CO₂-induced ocean acidification. *Geology* 37, 1131–1134.
- Rosa, R., Seibel, B.A., 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *Proc. Natl. Acad. Sci. U. S. A.* 105, 20776–20780.
- Sanders, M.B., Bean, T.P., Hutchinson, T.H., Le Quesne, W.J.F., 2013. Juvenile King Scallop, *Pecten maximus*, is potentially tolerant to low levels of ocean acidification when food is unrestricted. *PLoS One* 8 (9), e74118. <http://dx.doi.org/10.1371/journal.pone.0074118>.
- Schiffer, M., Harms, L., Poertner, H.O., et al., 2014. Pre-hatching seawater pCO₂ affects development and survival of zoea stages of Arctic spider crab *Hyas araneus*. *Mar. Ecol. Prog. Ser.* 501, 127–139.
- Seibel, B.A., 2007. On the depth and scale of metabolic rate variation: scaling of oxygen consumption and enzymatic activity in the class Cephalopoda (Mollusca). *J. Exp. Biol.* 210, 1–11.
- Small, D., Calosi, P., White, D., Spicer, J.I., Widdicombe, S., 2010. Impact of medium-term exposure to CO₂ enriched seawater on the physiological functions of the velvet swimming crab *Necora puber*. *Aqua Biol.* 10, 11–21.
- Stern, N., 2006. *The Economics of Climate Change: The Stern Review*. Cambridge University Press.
- Styf, H.K., Skold, H.N., Eriksson, S.P., 2013. Embryonic response to long-term exposure of the marine crustacean *Nephrops norvegicus* to ocean acidification and elevated temperature. *Ecol. Evol.* 3, 5055–5065.
- Talmage, S.C., Gobler, C.J., 2010. Effects of past, present, and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. *Proc. Natl. Acad. Sci.* 107 (40), 17246–17251. <http://dx.doi.org/10.1073/pnas.0913804107>.
- Thomsen, J., Casties, I., Pansch, C., Körtzinger, A., Melzner, F., 2013. Food availability outweighs ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. *Glob. Change Biol.* 19, 1017–1027. <http://dx.doi.org/10.1111/gcb.12109>.
- Turley, C., Gattuso, J.-P., 2012. Future biological and ecosystem impacts of ocean acidification and their socioeconomic-policy implications. *Curr. Opin. Environ. Sustain.* 4, 1–9.
- Turley, C., Gattuso, J.-P., Hoegh-Gulberg, O., et al., 2011. Ocean acidification: examples of potential impacts. In: Richardson, K., Steffen, W., Liverman, D. (Eds.), *Climate Change: Global Risks, Challenges and Decisions*. Cambridge University Press, pp. 37–39.
- Van Colen, C., Debussche, E., Braeckman, U., Van Gansbeke, D., Vincx, M., 2012. The early life history of the clam *Macoma balthica* in a high CO₂ world. *PLoS One* 7, e44655.
- Vargas, C.A., Aguilera, V., San martin, V., Manríquez, P., Navarro, J., Duarte, C., Torres, R., Lardies, M., Lagos, N., 2014. CO₂-Driven ocean acidification disrupts the filter feeding behavior in Chilean gastropod and bivalve species from different geographic localities. *Estuaries Coasts* 38. <http://dx.doi.org/10.1007/s12237-014-9873-7>.
- Vengatesen, T., Ko, G., 2012. Larval growth response of the Portuguese oyster (*Crassostrea angulata*) to multiple climate change stressors. *Aquaculture* 370–371, 90–95.
- Walther, K., Anger, K., Pörtner, H.-O., 2010. Effects of ocean acidification and warming on the larval development of the spider crab *Hyas araneus* from different latitudes (54° vs. 79°N). *Mar. Ecol. Prog. Ser.* 417, 159–170.
- Walther, K., Sartoris, F.J., Bock, C., Pörtner, H.-O., 2009. Impact of anthropogenic ocean acidification on thermal tolerance of the spider crab *Hyas araneus*. *Biogeosciences* 6, 2207–2215.
- Walther, K., Sartoris, F.J., Pörtner, H.-O., 2011. Impacts of temperature and acidification on larval calcium incorporation of the spider crab *Hyas araneus* from different latitudes (54° vs. 79°N). *Mar. Biol.* 158, 2043–2053.
- Wang, Y., Li, L., Hu, M., Lu, W., 2015. Physiological energetics of the thick shell mussel *Mytilus coruscus* exposed to seawater acidification and thermal stress. *Sci. Total Environ.* 514, 261–272.
- Weiss, I.M., Tuross, N., Addadi, L., Weiner, S., 2002. Mollusc larval shell formation: amorphous calcium carbonate is a precursor phase for aragonite. *J. Exp. Zool.* 293, 478–491.
- Whiteley, N.M., 2011. Physiological and ecological responses of crustaceans to ocean acidification. *Mar. Ecol. Prog. Ser.* 430, 257–271.
- Williamson, P., Turley, C., Ostle, C., 2017. Ocean acidification. *MCCIP Sci. Rev.* 2017, 1–14. <http://dx.doi.org/10.14465/2017.arc10.001-oac>.
- Williamson, P., Turley, C., Brownlee, C., Findlay, H., Ridgwell, A., Schmidt, D., Schroeder, D., Blackford, J., Tyrrell, T., Pinnegar, J., 2013. Impacts of Ocean acidification. *MCCIP Sci. Rev.* 2013, 34–48.
- Wittmann, A.C., Pörtner, H.-O., 2013. Sensitivities of extant animal taxa to ocean acidification. *Nat. Clim. Change* 3, 995–1001. <http://dx.doi.org/10.1038/nclimate1982>.
- Wood, H.L., Spicer, J.I., Widdicombe, S., 2008. Ocean acidification may increase calcification rates, but at a cost. *Proc. R. Soc. B* 275, 1767–1773.
- Wootton, J.T., Pfister, C.A., Forester, J.D., 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multiyear dataset. *Proc. Natl. Acad. Sci. U. S. A.* 105, 18848–18853.
- Zheng, C., Jeswin, J., Shen, K., Lablache, M., Wang, K., Liu, H., 2015. Detrimental effect of CO₂-driven seawater acidification on a crustacean brine shrimp, *Artemia sinica*. *Fish Shellfish Immunol.* 43, 181–190.